

## SIZE-DEPENDENT TIMING OF METAMORPHOSIS IN MILKWEED BUGS (*ONCOPELTUS*) AND ITS LIFE HISTORY IMPLICATIONS

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The allocation of time and resources to the conflicting demands of growth and reproduction has been an important theme in evolutionary explanations for the diversity of life history patterns among living organisms (*c.g.*, Gadgil and Bossert, 1970; Schaffer, 1974). In examining the problem of how this allocation is achieved and adaptively modified under different ecological conditions, studies of organisms with discrete life stages are particularly important, since growth and reproductive phases of the life cycle are often clearly delineated. Further, an understanding of this problem requires the integration of ecological theory with developmental and physiological considerations. These points are well illustrated by Wilbur and Collins' (1973) attempt to model control of the neurohormonal processes underlying developmental plasticity in amphibians and to account for variation in amphibian life cycles. A salient feature of their model is the role of hypothetical mechanisms which allow larvae to monitor both their rate of growth and body size; information on which the decision to metamorphose is assumed to be based. Although the existence of such mechanisms in amphibians remains to be demonstrated, there is evidence to suggest that analogous models may be relevant to the study of adaptation in insect life cycles.

Mechanisms which influence development in response to changes in body size have been described in studies of the blood-sucking bug, *Rhodnius prolixus* (Wigglesworth, 1934; Van der Kloot, 1961; Steel and Harnsen, 1971). Molting occurs only after the ingestion of a blood meal, and these studies provide strong evidence that distension of the abdomen is detected by stretch receptors which initiate the molt by triggering the release of brain hormone. Further evidence of size-dependent regulation of insect development has come from experimentally manipulating growth of larvae of a holometabolous insect, *Manduca sexta*. Nijhout and Williams (1974a, b) have shown that 5th-instar larvae molt only when they attain a size corresponding to a weight of about 5 g. When this critical size is reached, the corpora allata cease to secrete juvenile hormone, initiating the endocrine events leading to the molt. The determination of which molt will lead to a pupa is also apparently made on the basis of size (Nijhout, 1975).

Here evidence is presented that molting in *Oncopeltus* nymphs is also initiated only when a critical size is attained. Viewed in an ecological context, it is suggested that size-dependent regulation of development in *Oncopeltus* represents a life history adaptation to unpredictable conditions for larval growth.

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## MATERIALS AND METHODS

Experiments were conducted with nymphs of *Oncopeltus cingulifer cingulifer*, a species of particular ecological interest because of its wide Neotropical distribution (Slater, 1964; O'Rourke, 1977). Stock cultures of *O. c. cingulifer* were derived from collections made in Trinidad. Since *O. fasciatus* has been the preferred species for physiological studies (Feir, 1974), some additional experiments were conducted with *O. fasciatus* nymphs, using a stock culture derived from collections made in Missouri, to determine whether comparable results can be expected from studies of this insect. Developmental times are the same for both species despite the smaller size of *O. c. cingulifer*. Under standard laboratory conditions described below, nymphs reach adult eclosion about 21 to 25 days after hatching. Newly-eclosed female *O. c. cingulifer* adults weigh 40 to 50 mg, compared with 60 to 70 mg for *O. fasciatus* females (Blakley, 1977).

Both species had been reared in the laboratory for several generations at the time these experiments were begun. In all experiments, nymphs were reared at 27° C under a 14L:10D photoperiod. Relative humidity varied between 30 and 60%. Details of culturing technique and experimental design are given in the appropriate sections below.

## RESULTS

*Competence of starved nymphs to complete development*

Previous investigations have shown that *O. fasciatus* nymphs starved in the late 5th (final) instar often complete development and undergo adult ecdysis (e.g., Barrett and Chiang, 1967). This was also observed in preliminary experiments conducted with *O. c. cingulifer* nymphs (Blakley, unpublished data). Results also suggested that body weight is an important factor in determining whether nymphs can successfully complete development under starvation conditions. For example, a few large nymphs starved at the time they entered the 5th instar subsequently molted, although smaller nymphs starved at later stages in this instar did not.

Further experiments were conducted to examine the relationship between body weight and the ability of starved nymphs to complete development. Five days after hatching, *O. c. cingulifer* nymphs were separated and reared individually in plastic petri dishes with holes punched in the lids to allow air circulation. Each nymph was provided with about 30 to 40 milkweed seeds (*Asclepias syriaca*) and a cotton-plugged vial of distilled water for drinking. Most nymphs entered the 5th instar 15 days after hatching, and at this time (Day 15) all nymphs were weighed and subsequently starved. Because nymphs are sensitive to desiccation (Barrett and Chiang, 1967), each bug was provided with a water vial. Only female nymphs were used, since there is a sexual dimorphism for body size. The sex of the 4th- and 5th-instar nymphs is easily determined by inspection of the abdomen (Johansson, 1958).

Results of this experiment revealed that 5th-instar nymphs whose weight exceeded 21 mg invariably completed development under starvation conditions (Fig. 1). At lower weights, progressively fewer nymphs did so, although they

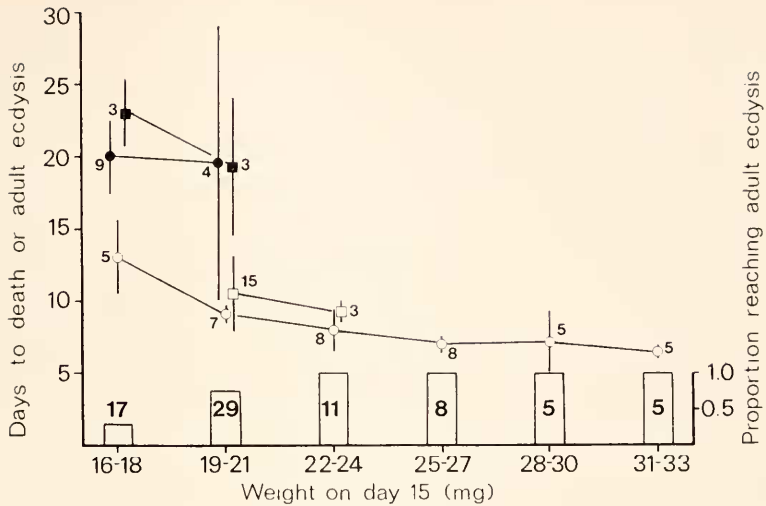


FIGURE 1. Consequences of starvation, in relation to body weight, for female 4th- and 5th-instar *O. c. cingulifer* nymphs starved 15 days after hatching. In each weight range, open symbols show the average subsequent time interval until adult ecdysis occurred. For nymphs in each weight range which did not undergo adult ecdysis, the average period for which they survived is represented by a closed symbol. Circles are averages for nymphs which were in the 5th instar on Day 15; squares are averages for nymphs which were in the 4th instar at this date. For each average, the number of nymphs represented is given and a vertical line indicates one standard deviation. Histogram shows the proportion of 4th- and 5th-instar nymphs reaching adult ecdysis in relation to body weight.

usually survived for much longer periods than was required for the completion of this instar. The importance of weight in determining whether a starved nymph would metamorphose was further emphasized by observations on nymphs which were still in the 4th instar on Day 15. Three nymphs weighing at least 22 mg subsequently molted to the 5th instar and later metamorphosed to the adult stage under starvation conditions. As with 5th-instar nymphs, the proportion of individuals completing development declined sharply at lower weights, and no 4th-instar nymphs weighing less than 19 mg reached the adult stage.

The same experiment, conducted with *O. fasciatus* nymphs, yielded comparable results (Fig. 2). As in the case of *O. c. cingulifer*, nymphs were weighed and starved on Day 15, when most nymphs entered the 5th instar. Again it was found that the proportion of nymphs which completed development declined sharply over a relatively narrow range of weights. Only 8 of 114 nymphs (7%) weighing less than 25 mg did so, while all 5th-instar nymphs weighing more than 29 mg subsequently molted. Of the 4th-instar nymphs weighing 25 to 29 mg on Day 15, 25% eventually reached the adult stage, as did 16% of the 49 nymphs in this instar weighing 20 to 24 mg. Observations made on male nymphs in this experiment gave very similar results (Fig. 3), although the proportion of 5th-instar nymphs weighing less than 30 mg which molted was slightly higher for males (17%) than for females (9%).

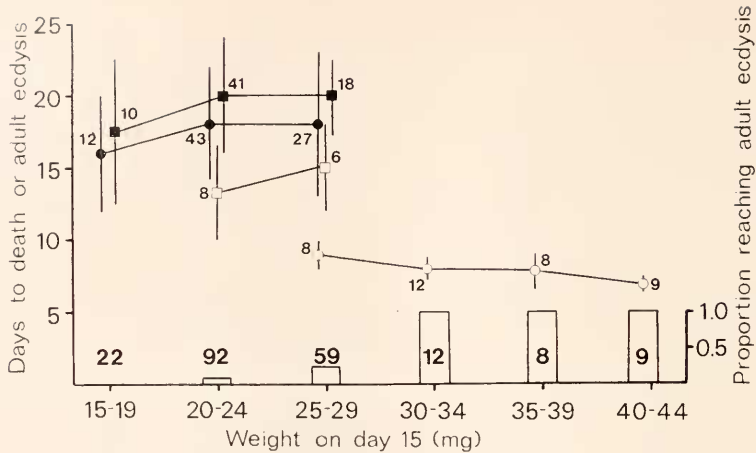


FIGURE 2. Effects of starvation from Day 15 on female *O. fasciatus* nymphs. Symbols and conventions are as in Figure 1. Note that, in contrast with *O. c. cingulifer* females, few nymphs weighing less than 30 mg completed development.

The ability of some starved 4th-instar nymphs to molt to the 5th instar and, without feeding at any time during this instar, later eclose as adults, clearly demonstrates that starvation does not invariably interrupt the normal sequence of development. It is suggested that the effect of starvation on smaller nymphs is to prevent them from reaching a critical size, at which they become competent to undergo adult ecdysis subsequently. Results for *O. c. cingulifer* females (Fig.

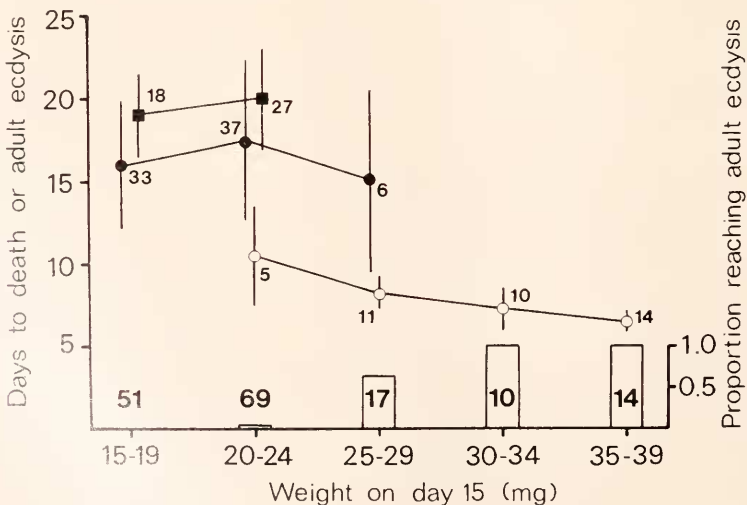


FIGURE 3. Effects of starvation from Day 15 on male *O. fasciatus* nymphs. Symbols and conventions are as in Figure 1. Note the larger proportion of nymphs in the 25 to 29 mg range which completed development in comparison with females (Fig. 2).

1), for example, are thus interpreted as follows. Nymphs entering the 5th instar at a weight of less than 19 mg which failed to metamorphose had not attained a critical size, so that without further growth they were not competent to complete development. Even a small increase in size due to the ingestion of water might allow some small nymphs to attain this size after Day 15; this may explain why five nymphs weighing about 18 mg did metamorphose. A critical size had been attained by nymphs weighing at least 22 mg and these nymphs were competent to complete development even under starvation conditions. Evidently the critical size corresponds to a weight of about 19 to 21 mg. Note that 21 4th-instar nymphs had attained this weight by Day 15 and that all but three subsequently completed development. Nymphs which attain the critical weight for metamorphosis while still in the 4th instar would, on entering the 5th instar, be competent to undergo adult ecdysis subsequently without further growth. If the critical size is taken as the minimum weight range in which at least 50% of the nymphs completed development, the values for *O. fasciatus* females (Fig. 2) and males (Fig. 3) are 30 to 34 and 25 to 29 mg, respectively. These differences are not surprising, in view of the fact that *O. fasciatus* is a larger bug, and that female *Oncopeltus* are larger than males.

#### *Experimental prolongation of the 5th instar*

To demonstrate that the timing of adult ecdysis is determined by the attainment of a critical size, further experiments were conducted with *O. c. cingulifer*

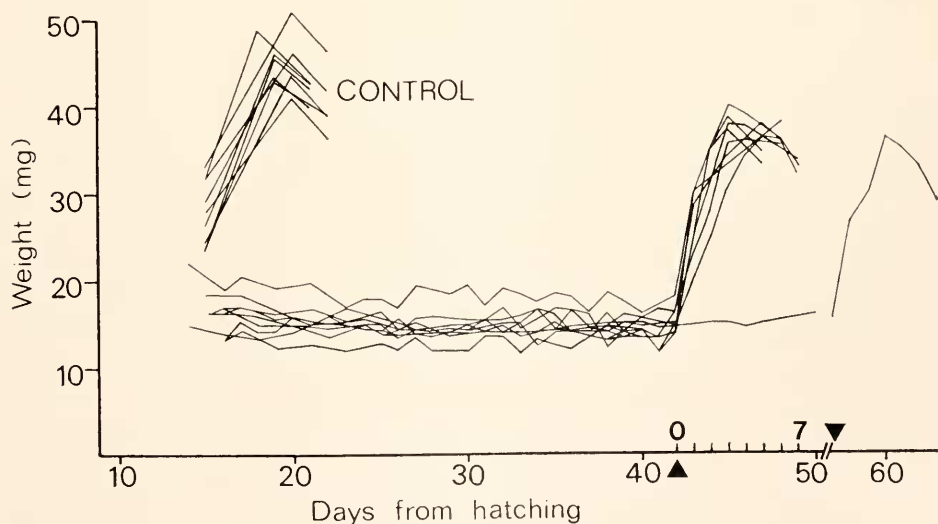


FIGURE 4. Experimental prolongation of the 5th instar of female *O. c. cingulifer* nymphs by maintaining weight below 20 mg. Each line represents a growth curve for one nymph, beginning on the day it entered the 5th instar. The final weight shown in each growth curve is that of the newly-eclosed adult. Triangles on the abscissa indicate the time at which nymphs resumed continuous feeding. Control group was allowed to feed normally throughout the 4th and 5th instars.



nymphs. Initially nymphs of both sexes were reared as in the previous experiments. Milkweed seeds were removed when a nymph's weight exceeded about 10 mg, although drinking water was supplied. All nymphs subsequently molted to the 5th instar. Nymphs of both sexes were then maintained at a weight of about 15 to 18 mg by allowing them to feed for only 10 to 30 min daily. Nymphs reaching the upper limit of this weight range were starved until their weight dropped.

Adult ecdysis was prevented in the case of female nymphs, provided they did not exceed a weight of about 20 mg (Fig. 4). To demonstrate that they were capable of molting if allowed to exceed this weight, each nymph was provided with 20 to 30 milkweed seeds on Day 42. Following the resumption of growth, all nymphs metamorphosed within 5 to 7 days (Fig. 4). The relatively small sample size reflects the fact that few nymphs survived for this length of time. Of 70 females used, 55 died before Day 42. In addition, six nymphs metamorphosed before Day 42, after their weight was inadvertently allowed to exceed 20 mg. Evidently, metamorphosis is delayed indefinitely if nymphs do not attain a critical size. In an earlier experiment, one nymph was maintained below this size until day 57 (Fig. 4).

In 14 cases, male 5th-instar nymphs were also successfully maintained below 20 mg, yet all but three molted before Day 42; adult ecdysis ensued if they attained a weight of at least 17.5 mg. This result is consistent with the lower value for the critical weight suggested for *O. fasciatus* males relative to females.

#### *Timing of ecdysis in plant-fed bugs*

Ralph (1976) and Root and Chaplin (1976) have shown that *O. fasciatus* and *O. c. cingulifer* nymphs reared on milkweed plants, rather than seeds, exhibit slow growth and development. Prolonged development under these conditions may reflect the additional time required for slow-growing nymphs to reach a critical size for molting. This possibility was investigated by observing the growth and development of individual nymphs on flowering milkweed plants (*Asclepias curassavica*) at the same temperature and photoperiod as in previous experiments. Female *O. c. cingulifer* nymphs were reared on milkweed seeds and transferred to milkweed plants 2 to 4 days after entering the 4th instar (typically lasting 4 to 5 days). Each nymph was subsequently weighed daily until adult ecdysis occurred. On entering the 5th instar, some nymphs were again provided with seeds, while the majority continued feeding on plants.

Results of these experiments are consistent with the hypothesis that metamorphosis occurs only after a critical size is attained. From previous experiments (Figs. 1, 4), this size is expected to correspond to a weight of about 20 mg in the case of female *O. c. cingulifer* nymphs. Growth curves of 5th-instar nymphs from the present experiments are illustrated in Figure 5; complete results are summarized in Figure 6. Nymphs which entered the 5th instar at a weight of at least 20 mg metamorphosed 6 to 8 days later, regardless of whether they fed on seeds or plants during this instar. Since this was also usually true of starved nymphs (Fig. 1), these results were as expected. Moreover, nymphs which entered the 5th instar at a weight of less than 20 mg, and which were then

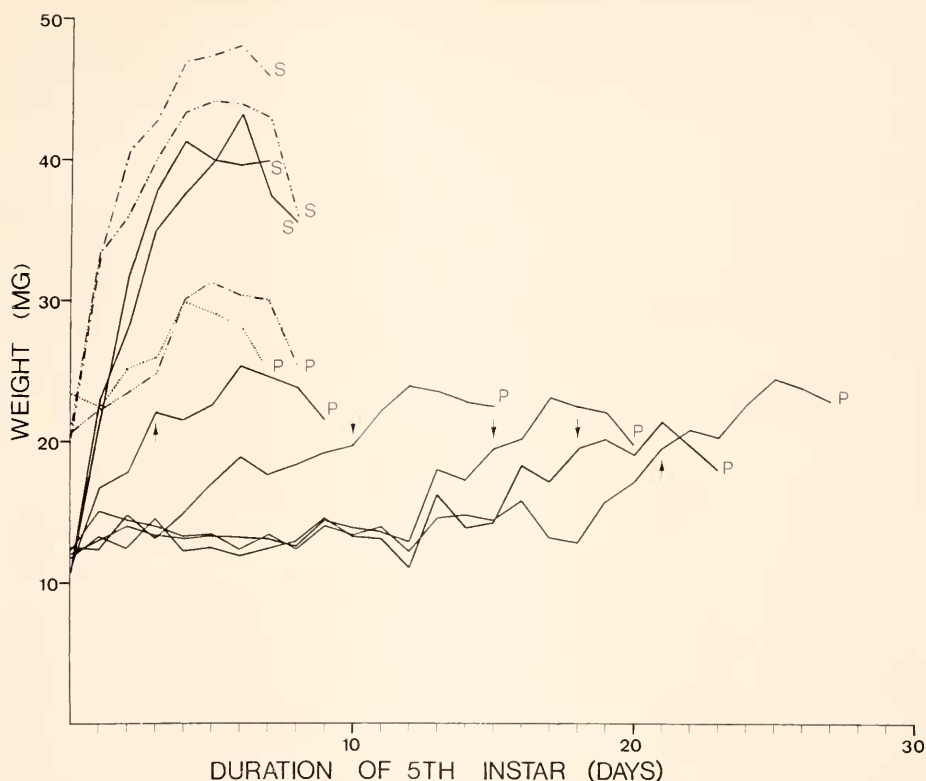


FIGURE 5. Growth curves for individual 5th-instar nymphs which fed in this instar either on milkweed seeds (S) or milkweed plants (P), showing the temporal relationship between the attainment of a critical weight of about 20 mg and subsequent adult ecdysis (the latter indicated by the final weight in each curve, which is that of the newly-eclosed adult). Nymphs which exceeded 20 mg at the outset of the 5th instar (stippled curves) metamorphosed 6 to 8 days later. Differences in diet had no effect on this time interval. Nymphs which weighed less than 20 mg at the outset of the 5th instar (solid curves) were able to attain this weight within 24 hr if fed seeds, and these nymphs also metamorphosed within a similar time interval. A longer and variable length of time was required to attain a weight of 19.5 to 20.0 mg if they were fed instead on plants. However, once this weight was attained (arrows), adult ecdysis ensued within 5 to 7 days. See Figure 6 for complete results of these experiments.

provided with seeds, attained this weight within 24 hr and also metamorphosed 6 to 8 days later (Figs. 5, 6). Note also that nymphs reared on seeds throughout their development which exceed 20 mg on entering the 5th instar typically metamorphose 6 to 7 days later (Fig. 4). Thus, under a variety of experimental conditions, nymphs weighing at least 20 mg at the outset of the 5th instar subsequently metamorphose within a relatively narrow period of 6 to 8 days.

In contrast, the duration of the 5th instar was highly variable in the case of nymphs which entered this instar at less than 20 mg and which fed only on plants.

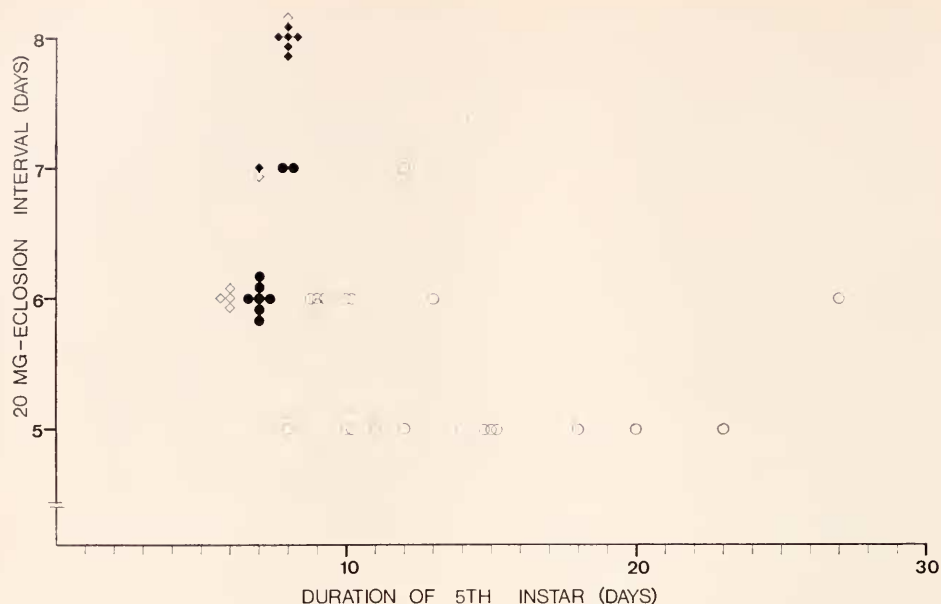


FIGURE 6. Complete results of experiments described in Figure 5. Timing of adult ecdysis is plotted in relation to two events, the time at which nymphs entered the 5th instar (abscissa) and the time at which they attained a weight of 19.5 to 20.0 mg (ordinate). *Diamonds* represent nymphs which weighed more than 20 mg at the outset of the 5th instar; the two time intervals are thus equivalent here. These nymphs metamorphosed after 6 to 8 days, whether reared on seeds (closed diamonds) or plants (open diamonds). *Circles* represent nymphs which weighed less than 20 mg at the outset of the 5th instar. These nymphs attained this weight within 24 hr and metamorphosed 6 to 7 days later when fed seeds (closed circles). When fed plants instead, the duration of the 5th instar varied considerably (8 to 27 days; open circles). However, in relation to the time at which a weight of 19.5 to 20.0 mg was attained, the timing of metamorphosis was relatively invariant (5 to 7 days later). Variation in the duration of the 5th instar is thus largely a reflection of individual differences in the time required to attain a weight of about 20 mg.

However, this variation largely reflects individual differences in the time required to attain a weight of 19.5 to 20.0 mg; all nymphs metamorphosed 5 to 7 days after reaching this weight (Fig. 6). This same interval of 5 to 7 days between the time this weight was attained and subsequent metamorphosis was also observed in the case of partially starved nymphs which resumed growth on Day 42 (Fig. 4). The reason for the slight difference between this 5 to 7 day interval and the 6 to 8 day interval observed in the case of nymphs exceeding 20 mg at the outset of the 5th instar is not known.

These results demonstrate that the existence of a critical size for molting provides an explanation for the prolonged development of slow-growing nymphs feeding on plant tissues. However, observations made on nymphs reared on milkweed plants from hatching, under the same environmental conditions as before, reveal greater flexibility in development than indicated in previous experiments. Although there was considerable variation in the duration of the 5th



TABLE I

Comparison of size, growth and developmental times for female 5th-instar nymphs reared from the 4th instar on plants or reared from hatching on plants.

Treatment	N	Pronotal width* (mm)	Duration of 5th instar (days)	Weight** (mg)		
				Day E-5	Day E-6	Day E-7
Transferred to plants in 4th instar	21	$\bar{x}$ 2.1	13.3	21.4	19.5	17.4
		Range 2.0-2.2	8-27	19.5-25.0	16.5-25.8	14.4-22.3
Reared from hatch- ing on plants	13	$\bar{x}$ 1.8	11.4	15.6	13.7	13.0
		Range 1.7-1.9	7-14	12.4-21.8	11.7-18.5	9.1-18.0

\* Measured on newly-molted 5th-instar nymphs using dissecting microscope with eyepiece graticule.

\*\* Weight of 5th-instar nymphs at 5, 6, and 7 days before adult eclosion.

instar, with one exception these nymphs did not attain a weight of about 20 mg or more at 5, 6, or 7 days prior to adult eclosion (Table I). The discrepancy between these results and those obtained using nymphs transferred to plants in the 4th instar may be a reflection of the morphological dissimilarity between the 5th instar nymphs produced in the two experiments. This dissimilarity is clearly seen, for example, in measurements of pronotal width (Table I) and in other morphological features, such as antennal length, whose dimensions do not change with growth during the 5th instar. If the critical size is determined by nymphs in relation to some fixed morphological dimension, it will correspond to a similar weight for all nymphs only if they are morphologically similar. The markedly smaller 5th-instar nymphs obtained by rearing them from hatching on plants would then be expected to metamorphose after attaining a relative critical size which corresponds to a lower weight than 20 mg.

## DISCUSSION

Results presented here are consistent with the hypothesis that 5th-instar *Oncopeltus* nymphs are able to assess their body size and that when a critical size is attained, physiological processes are initiated which lead to adult ecdysis. Although the nature of these processes has not been examined in this investigation, there is evidence from studies of 5th-instar *O. fasciatus* nymphs that stretch receptors are involved in their initiation at a critical size (F. Nijhout, Duke University, in preparation). That our experiments concern only the size-dependent timing of adult ecdysis does not imply that this phenomenon is unique to that particular molt. Preliminary results suggest that size may also play a similar role in the timing of earlier molts (Blakley, unpublished data).

Delayed molting under nutritional conditions which impose slow growth may effectively result because of the need to attain a critical size. In contrast, the critical weight of about 20 mg for adult ecdysis in female *O. c. cingulifer* nymphs, for example, may be attained by rapidly-growing nymphs even before they enter the 5th instar, as indicated by the weights of some 4th-instar nymphs in Figure 1.

Provided the critical weight is attained or exceeded at the outset of the 5th instar, the timing of metamorphosis is unaffected by further growth and invariably occurs 6 to 8 days later.

The fact that the critical weight for adult ecdysis may be attained by nymphs in the late 4th instar raises the problem of what determines the nature of a molt. If body size plays a role in determining which molt results in metamorphosis to the adult stage (*cf.* Nijhout, 1975), why do such 4th-instar nymphs not subsequently metamorphose as adults, rather than molting to the 5th instar? Since rapidly-growing nymphs do not attain a weight of 20 mg until 3 to 4 days after entering the 4th instar, which has a duration of 4 to 5 days (Blakley, unpublished data), it is suggested that the nature of the following molt has already been determined by the late 4th instar, and is unaffected by subsequent changes in size (or weight). Although it would be of interest to observe the effect on the following molt if a nymph attained a weight of 20 mg at the outset of the 4th instar, it seems unlikely that nymphs could ever attain this size so early in their development.

Milkweed bugs in the *Erythriscius* subgenus (including *O. fasciatus* and *O. cingulifer*) have a Neotropical distribution, with the exception of some migrant populations of *O. fasciatus* (O'Rourke, 1977). Tropical host milkweeds of these insects, notably *A. curassavica*, are an unreliable source of seeds because of their asynchronous phenology (Root and Chaplin, 1976; Blakley, 1977). As a consequence, nymphs are confronted with the possibility at any time in their development that seeds may be unavailable on a host plant, forcing them to feed on other plant structures (Blakley, in preparation). These considerations suggest that development of nymphs under natural conditions is influenced by factors affecting growth which may vary unpredictably.

In this context, size-dependent initiation of molting provides a means of adjusting the timing of life history events to prevailing ecological conditions. Since the reproductive success of adults is positively correlated with body size at eclosion (Blakley, 1977), it may be advantageous for small nymphs to delay molting and thus obtain additional time for further growth. Evidence from studies of 5th-instar nymphs previously reared on plants for different lengths of time (Table 1) suggests that long delays in development of nymphs which do not have access to seeds in early instars may be avoided by adjustments in the size below which molting is delayed. If this interpretation is correct, further studies of the relationship between growth and subsequent morphological size in the following instar will be required to determine how this is accomplished.

While the relationship between adult body size and reproductive success suggests an explanation for the role of body size in the timing of metamorphosis, there are also obvious disadvantages in prolonging the larval period, because of increased pre-adult mortality. Depending on the relative advantages and disadvantages, the size at which molting is initiated may be modified by natural selection. Evidence of geographic variation in body size in *O. fasciatus* and other species (Blakley, Dingle and Klausner, in preparation) suggests that such modifications have occurred in different selective environments. This issue will be examined in a future communication.

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#### SUMMARY

Experimental alteration of growth of *Oncopeltus* nymphs suggests that adult ecdysis occurs only after a critical size (indexed by weight) is attained. Nymphs which exceed this size at the outset of the 5th (final) instar metamorphose 6 to 8 days later. Nymphs which attain this size later in the 5th instar subsequently metamorphose 5 to 7 days later.

Studies of *O. c. cingulifer* and *O. fasciatus* suggest that interspecific differences in adult body size provide an indication of differences in the critical size for metamorphosis. Further, sexual dimorphism in body size also indicates a dimorphism in the critical size for metamorphosis.

The ability of *Oncopeltus* nymphs to assess their size provides a means of adjusting development in response to variable conditions affecting growth. Delayed metamorphosis in slow-growing nymphs provides additional time for further growth. This effect may be advantageous, since reproductive success declines with decreasing adult body size.

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